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Morphology and histology of the reproductive system in females of the black field cricket *Teleogryllus commodus* WALKER 1869 (Insecta: Orthoptera): a drawing study

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A b s t r a c t : The reproductive system of the female black field cricket *Teleogryllus commodus* was investigated in morphological and histological respects, producing various drawings from light- and electron-microscopic observations. As a characteristic for orthopteran insects, the reproductive system of the studied species consists of paired ovaries, the lateral oviducts, the median oviduct, the spermatheca including a single receptacular complex (receptaculum seminis and ducuts receptaculi), the genital chamber as well as the accessory glands being characterized by a valuable number of ramifications. After insemination of the oocytes in the genital chamber, release of the eggs takes place by an ovipositor. Single structures of the reproductive system are constructed according to a basic architecture which includes, from outside to inside, a muscle layer, the basal membrane, a one-layer epithelium, and a cuticular intima. Regarding the receptaculum seminis and the accessory glands, the intima forms spiny to hair-like processes that support the transport of the spermatozoa and the lipophilic gland secretion, respectively.

K e y w o r d s: Reproductive system, ovary, oviduct, spermatheca, accessory glands, cricket, *Teleogryllus commodus*.

Introduction

Besides three pairs of locomotoric extremities, especially the three-part anatomy (caput, thorax, abdomen) may be regarded as a remarkable characteristic of insects, whereby the abdomen contains essential organs of the digestive and excretory system as well as those structures exclusively serving for reproduction. Concerning female insects, the reproductive system generally consists of paired ovaries, the lateral oviducts, the median (unpaired) oviduct, the genital chamber, the spermatheca, and the accessory glands (e. g. SNODGRASS 1935, WIGGLESWORTH 1972, CHAPMAN 1998). The ovaries are commonly situated dorsal or lateral to the gastrointestinal tract and include a multiple number of ovarioles, within which the oogenesis, i. e. the developmental process of the oocytes, is located (e. g. WEBER & WEIDNER 1978). The oviducts are characterized by their tubular shapes and a basic morphology with a one-layer epithelium, a basal membrane, and an outer muscle coat. Within some insect orders such as the Acridoidea, gland cells are contained in specific segments of the oviducts (CHAPMAN 1998). The lateral oviducts emanating from the ovaries are joined directly anterior to the genital chamber, thereby

forming the median oviduct. This structure is usually characterized by an additional cuticular layer (KAULENAS 1992, CHAPMAN 1998). The median oviduct opens into the genital chamber at the 8th abdominal segment, where the insemination of the oocytes transferred from the ovaries is conducted. The ectodermal spermatheca, i. e. the organ complex serving for the storage of spermatozoa transferred from the male during copulation, is connected to the median oviduct or to the genital chamber. Depending upon the insect order, it is composed of a variable number of receptacula seminis (STURM 2005). The ectodermal accessory glands completing the reproductive tract also open into the genital chamber. In those insect orders, within with the glands are not subject to a secondary reduction, the structures are characterized by high variability concerning their shape and morphology (e. g. BRUNET 1952, STURM & POHLHAMMER 2000). A similar variability may be stated for the function of the gland secretion, which, among others, is required for the formation of the egg shells, for cocoon production or, in the case of insects with an ovipositor, as a lubricant (STURM & POHLHAMMER 2000).

Within the insect order of the Orthoptera the construction scheme of the reproductive tract outlined above is fully realized, whereby in most families and in paticular among the gryllids egg-laying is carried out via an ovipositor. The spermatheca contains a single receptaculum seminis (e. g. ESSLER et al. 1992, STURM 2003), and the accessory glands, as far as preserved, produce a lipophilic secretion, whose main task includes the facilitated transport of the inseminated eggs through the ovipositor. Oviposition of practically all orthopteran species is strongly affected by external factors, among which environmental temperature has an enhanced significance (STURM 2002, 2008).

In the contribution presented here a detailed insight into the female reproductive system of the black field cricket *Teleogryllus commodus* WALKER 1869 with all its specificities is provided. For a successful execution of the study diverse histological and microscopic methods were applied, which besides the description of the external morphology of single reproductive organs also allowed a comprehensive documentation of respective cell structures.

Materials and Methods

Culture and keeping of Teleogryllus commodus

Teleogryllus (Fig. 1) was reared and kept in a specifically equipped climate chamber at the former Institute of Zoology, University of Salzburg. As already outlined in detail by STURM (1999, 2008), crickets were fed with fresh lettuce, standard diet for labour animals (Altromin 1222), and water offered by moistened cotton pads. During experimental work environmental parameters in the climate chamber were set to the following constant values: air temperature: 25 °C, relative humidity: 60 %, photoperiod: 12 h. Those females used for the present study were kept in glass vessels with a standard volume of 5 litres, into which some nutrients as well as several sheets of paper for shelter had been transferred before.

Microscopic preparation and histological methods

For light-microscopic investigations selected animals were first anaesthetized in a stream of carbon-dioxide and afterwards decapitated. Studies concerning the determination of the external morphology of single reproductive structures were conducted by transferring

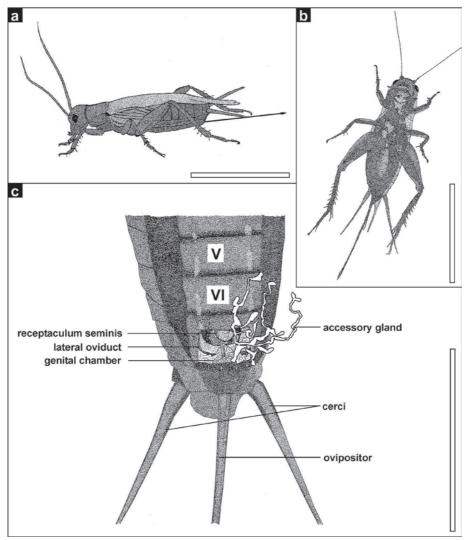


Fig. 1: (a) Female of the black field cricket *Teleogryllus commodus* WALKER 1869, lateral view (bar: 1 cm). (b) Ventral view of the female with the typical segmental organization of the abdomen (bar: 1 cm). (c) Terminal segments of the abdomen with a window cut into segment 7 (bar: 5 mm).

the abdomen into a preparation tube filled with insect Ringer's solution (STURM & POHLHAMMER 2000) and opening its ventral side at the 7^{th} and 8^{th} segment. Single organs

such as the accessory glands were separated and investigated by interference-contrast microscopy. For an appropriate determination of the organs' internal structure histological sections were produced. This methodic step was realized by dehydrating the abdomina of selected females in an alcohol series with increasing concentration of C_2O_5OH (50-100 %) and their subsequent fixation in Bouin solution. The production of thin sections was conducted by embedding the fixed objects in epoxy resin, thereby varying the consistence of the embedding medium according to the predominance of cuticular structures in the epidermis and single organs. Sections were mounted on glass slides (76 × 26 mm). After dissolution of the embedding medium, sections were subject to Goldner, Azan or methylen-blue staining (ADAM & CZIHAK 1964). Finally, preparations were treated with Canada balsam (n = 1.54) and covered up with a thin glass plate.

For the electron-microscopic performance the genital tract of a pre-selected female cricket was separated and subject to a 3-hour fixation in a mixture of paraformaldehyde and glutaraldehyde (KARNOVSKY 1965). In the case of SEM investigations, the fixed object was washed in cacodylate buffer, dehydrated in an alcohol series with increasing C₂H₅OH concentration and finally submitted to a critical-point drying process. For microscopic work the preparation was covered with a carbon film and sputtered with gold. Documentation of the object took place with a Cambridge 250 SEM selecting an accelerating voltage of 10 to 30 kV. For an appropriate performance with the TEM the fixation procedure had to be modified as follows: After fixation of the object with KARNOVSKY solution (see above) the structures of interest was post-fixed in osmium-tetroxide (1 %) for another 2 hours. Organs fixed in this way were washed in cacodylate buffer and dehydrated in an alcohol series with increasing C2H5OH concentration. Structures were afterwards embedded in epoxy resin (Epon 812), and ultrathin sections necessary for microscopic work were produced with a Reichert OM-U2 microtome and stained with uranyl-acetate and lead-citrate. Microscopic documentation was conducted on a Philips EM 300 selecting an accelerating voltage of 80 kV.

Results

Position and external morphology of single structures in the female reproductive system

Except for the ovaries and the lateral oviducts single organs of the reproductive system of *Teleogryllus* are commonly located within the abdominal segments 6 to 8 (Fig. 1c, 2). Thereby the caudal part of sternite 8 is transformed to the so-called subgenital plate. The ovaries are situated in the centre of the abdomen taking a position lateral to the digestive system. The lateral oviducts are joined to the median oviduct directly anterior to the genital chamber (Fig. 2a), and in further consequence the unpaired oviduct runs over a distance of another 2 mm in caudal direction. Regarding its dimensions the genital chamber offers space for only one oocyte, which is released from the reproductive system via the ovipositor (Fig. 1, 2).

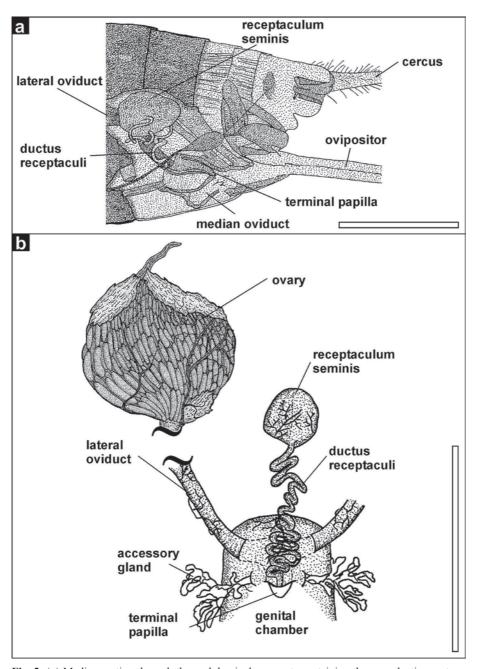


Fig. 2: (a) Median section through those abdominal segments containing the reproductive system. The accessory glands positioned more laterally are not visible in this view (bar: 2 mm). (b) Illustration exhibiting the organ arrangement of the reproductive system in orthopteran insects (bar: 2 mm).

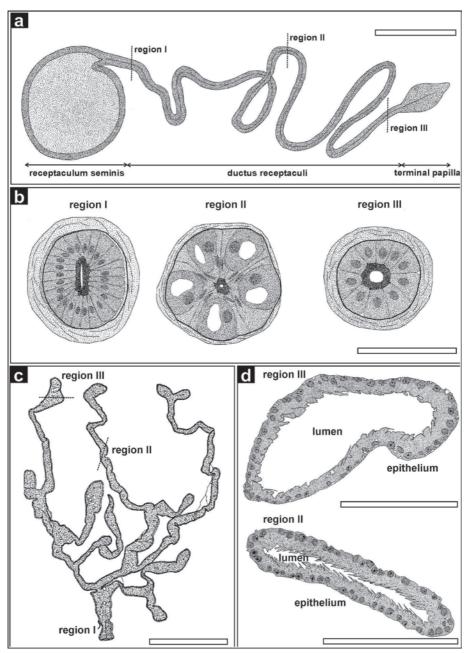


Fig. 3: (a) Morphological organization of the receptacular complex in female *Telegryllus* (bar: 0.5 mm). (b) Cross sections through the morphologically distinguishable regions of the ductus receptaculi (bar: 0.1 mm). (c) External shape of an accessory gland occurring in females of the black field cricket (bar: 2 mm). (d) Cross sections through the apical region III and the middle region II (bars: 0.5 mm).

The receptacular complex is characterized by a highly remarkable outer morphology due to its 25 mm long and 0.1 mm thick, strongly wound ductus and its globular receptaculum seminis having a diameter of about 0.5 mm (Fig. 3a). In streched condition the length of the ductus clearly exceeds that of the whole animal. The ductus opens into the genital chamber via the so-called terminal papilla, a stylus-like structure (Fig. 2 a). The spermatozoa released from the receptacular complex are transferred to the micropyles, i. e. the dorsal entrance pores of the oocytes to be inseminated, via a specific seminal gutter. An interesting external morphology may be also stated for the accessory glands reaching a maximum length of 12 mm in *Teleogryllus* and being characterized by a highly ramified shape (Fig. 2b, 3c). The glands' ramifications following a basal region form a complex ductal system, which is responsible for the transfer of the apically produced secretion to the opening of the structure into the genital chamber. The accessory glands are commonly positioned lateral to the terminal papilla (Fig. 2b). Their basal region is covered by a muscle coat serving for an active release of the secretion or the closure of the organ during sexual inactivity (Fig. 8a).

Histology of the reproductive organs

Single reproductive structures of Teleogryllus are partly characterized by a highly specific histology. The lateral oviducts consist of an outer muscle laver, a basal membran measuring 2 µm in thickness, and a 40 to 70 µm high cylindrical epithelium. Concerning the median oviduct, this construction scheme is extended by an endocuticular layer with a thickness of several milimetres, underlining the ectodermal origin of this ductal section (Fig. 4b). The histo-morphological architecture stated for the oviducts may be also determined with slight modifications for the receptacular complex. Hence, the wall of the receptaculum seminis does not include a mucle layer with comparable thickness, but among other is composed of a mighty endocuticula forming processes 10 to 20 µm in length (Fig. 6a, b). Their preferential function consists in the support of the transport of male germ cells out of the organ. In histo-morphological respects the ductus receptaculi is marked by a clear subdivision into three parts (Fig. 3a, 4a, 5). Whilst the distal (Dr₃) and proximal (Dr₁) section of the ductus consist of a one-layer epithelium 15 to 30 µm in height, which is commonly surrounded by an outer muscle coat and demarcated from the inner lumen by a 4 to 8 µm thick cuticular intima, the middle glandular section (Dr₂) exhibits a more complex architecture. Here, the epithelium is composed of two different cell types, i. e. the gland cells and the cuticula-forming cells, both reaching a maximum height of 40 µm. The secretion produced in the gland cells is released into the lumen by passing the 10 µm mighty cuticular intima over a complex system of canals. According to recent hypotheses, the secretion mainly supports the transfer of spermatozoa into and out of the receptaculum, but also a cell-conserving function is discussed. Due to the external muscle coat being wrapped around the whole ductus the structure is enabled to execute peristaltic contractions, with the help of which spermatozoa are pumped into and out of the receptaculum. The accessory glands dispose of a similar structural complexity as the single constituents of the receptacular complex (Fig. 3d, 5). Analogous to the ductus receptaculi, these organs also reveal three regions (basal, middle, apical), among which only slight histo-morphological differences may be observed. Generally, each region is composed of a uniformly structured, one-layer epithelium that is demarcated from the coelom by a 0.2 to 1 µm thick basal membran and from the gland's lumen by a

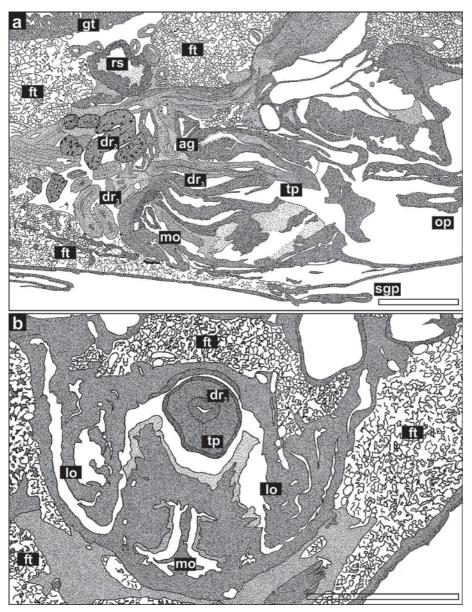


Fig. 4: (a) Median histological section through the terminal segments of the female abdomen with its essential reproductive structures (bar: 0.5 mm). (b) Cross section through the 7^{th} abdominal segment providing a detailed insight into the arrangement of several ductal structures (bar: 0.5 mm). Abbreviations: ag...accessory gland, dr2...ductus receptaculi, region II, dr3...ductus receptaculi, region III, ft...fatty tissue, gt...gut, lo...lateral oviduct, mo...median oviduct, op...ovipositor, rs...receptaculum seminis, sgp...subgenital plate, tp...terminal papilla.

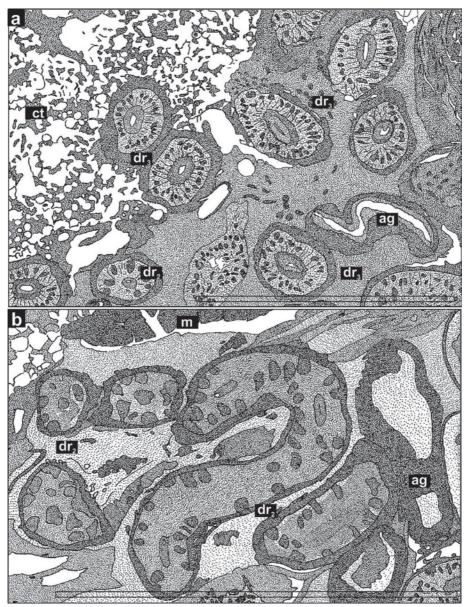


Fig. 5: Detailed views of some essential structures within the reproductive system of female *Teleogryllus*. (a) Different cross sections of the ductus receptaculi exhibiting a typical one-layer epithelium being demarcated from the glandular lumen by a more or less thick cuticular intima (bar: 0.5 mm). (b) Cross sections through the middle region of the ductus receptaculi with its glandular charcteristics (bar: 0.5 mm). Abbreviations: see Fig. 4, additional abbreviation: m...muscle tissue.

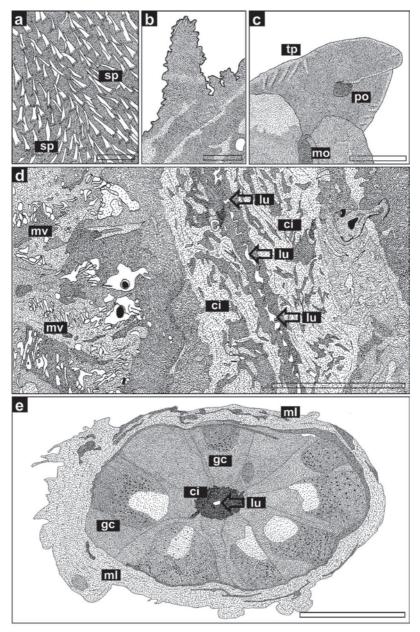


Fig. 6: Detailed morphology and histology of selected reproductive structures. (a) Internal surface of the receptaculum seminis with its numerous spines (sp; bar: $10~\mu m$). (b) Cuticular process in the receptaculum (bar: $10~\mu m$). (c) Detailed view on the terminal papilla (tp) and the orifice of the median oviduct (mo; bar: 0.1~m m). (d) Ultrastructure of region I of the ductus receptaculi (bar: $5~\mu m$). (e) Cross section through region II of the ductus (bar: $30~\mu m$). Additional abbreviations: ci...cuticular intima, gc...glandular cell, lu...lumen, ml...muscle layer, mv...microvilli.

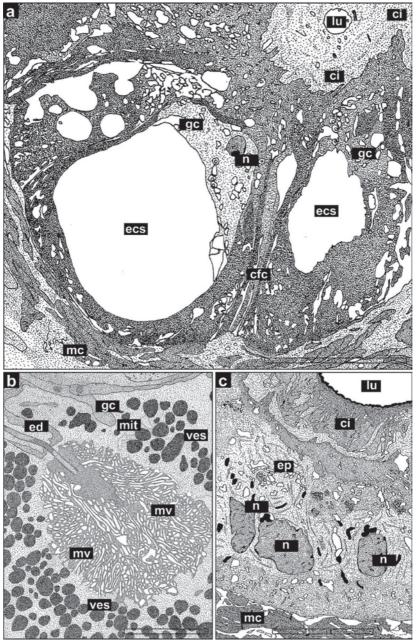


Fig. 7: (a) Detailed cellular structure of the glandular region II of the ductus receptaculi (bar: $10~\mu m$). (b) End apparatus of a glandular cell within region II of the ductus (bar: $3~\mu m$). (c) Cellular ultra-structure of region III of the ductus (bar: $10~\mu m$). Additional abbreviations: cfc...cuticula-forming cell, ecs...extracellular space, ed...efferent ductule, ep...epithelium, mc...muscle coat, mit...mitochondrium, n..nucleus, ves...vesicle.

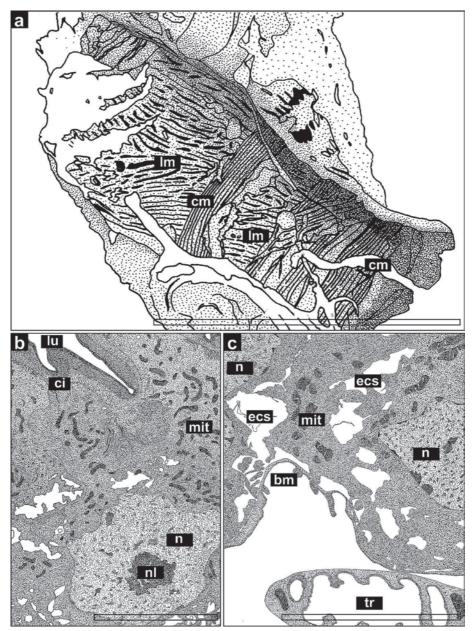


Fig. 8: (a) Most basal region of the accessory gland with the duct being covered with a muscle coat containing circular (cm) and longitudinal (lm) muscle fibres (bar: 1 mm). (b) Typical appearance of a single cell within the tissue of the accessory gland (bar: $10 \mu m$). (c) Basal part of the gland's epithelium with a basal membrane (bm) demarcating the epithelium from the coelom (bar: $10 \mu m$). Additional abbreviations: nl...nucleolus, tr...tracheole.

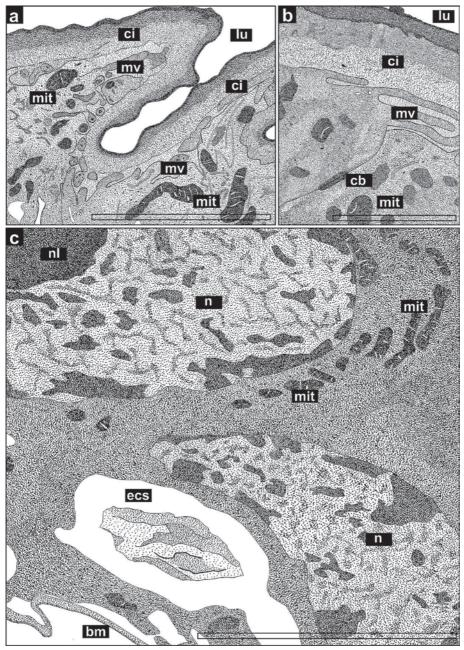


Fig. 9: Ultrastructure of the apical part of an accessory gland cell with its typical arrangement of the microvilli and the three-layer cuticula (bar: 5 μ m). (b) More detailed view on the apical part (bar: 3 μ m). (c) Basal part of an accessory gland cell with an extensive formation of extracellular spaces (bar: 5 μ m). Additional abbreviation: cb: cell border.

cuticular intima. This endocuticula usually includes three layers, which partly form spiny to hair-like processes. Form basal to apical region the height of the epithelium increases continuously, thereby reaching a maximum of about 60 μ m in the terminal parts of the structure. A similar trend may be recognized for the endocuticular processes, increasing their lengths from 5 to 10 μ m in the basal region to 20 μ m in the apical region. At the gland's orifice the epithelium is coated by circular and longitudinal muscle fibres fulfilling the functions already described above (Fig. 8a).

Cellular ultrastructure of selected reproductive organs

Cellular ultrastructur was investigated in detail for the ductus receptaculi and the accessory glands (Figs 6-9). Concerning the ductus, cells belonging to different sections of this tubular structure are characterized by very specific architectures. Whilst cells of region I located close to the receptaculum are identical among each other, forming columnar compartments with a height of 20 to 30 µm and being demarcated from the lumen by a 5 µm thick cuticular intima (Fig. 6d), cells of the glandular region II may be subdivided into two categories, i. e. the glandular cells sensu stricto and the cuticula-forming cells (Fig. 6a, 7a, b). Both cell types are connected with the basal mebrane and vary between 30 and 40 µm in height. The gland cells contain a remarkable extracellular space, into which the cellular secretion is released (Fig. 7a). Passing of this liquid towards the ductal lumen takes place over the efferent ductule (Fig. 7b) and a complex canal system running through the 10 µm cuticular intima. In the area of the end apparatus the number of microvilli and mitochondria is strongly increased. The spherical nucleus is somewhat reduced in size and usually situated in the middle part of the cell (Fig. 7a). Regarding the cells of region III, cellular structure shows some similarities to that of region I. Analogous to the proximal section of the ductus, cells have a columnar shape with a maximum height of 20 µm and are demarcated from the lumen by a mighty endocuticula (up to 8 μm). Cell nuclei are rather uniformly shaped (diameter: about 5 μm) and preferentially situated in the basal part of the cells. Contrary to region I the lumen is rather wide (10 to 15 µm) allowing the passage of a high number of spermatozoa (Fig. 7c). The structural variety reported for the cells of the ductus receptaculi can not be observed for the cellular units of the accessory glands. Independent of the position within the gland, cells are uniformly structured, thereby containing a more basally situated nucleus (diameter up to 15 µm) with a significantly sized nucleolus (Fig. 8b, 9c), high amounts of smooth endoplasmatic reticulum that is chiefly concentrated in the apical cell part and an apical cell membrane transformed to a continuous layer of microvilli (Fig. 9a, b). Depending upon the secretory activity of a cell its basal membrane is marked by partly deep invaginations increasing the basal suface area for an enhanced uptake of proto-substances (Fig. 8c, 9c). Demarcation from the coelom is realized by a basement membrane varying from 0.2 to 1 µm in thickness. Between the cells and the gland's lumen a three-layer cuticular intima is intercalated, whose thickness may reach up to 8 µm. Analogous to the receptaculum seminis the intima forms spiny to hair-like processes with a maximum length of 15 µm (Fig. 8b, 9a). From basal to apical region structural modifications mainly concern epithelial height increasing from about 30 to 60 µm as well as the width of the lumen which is significantly enhanced in the terminal parts of the gland. As another specificity the basal part contains an additional muscle coat with a regular sequence of longitudinal and circular mucle fibres causing both the closure of the gland and peristaltic contractions (Fig. 8a).

877

Discussion

The reproductive system of the black field cricket with its various structures (ovaries, oviducts, receptacular complex, accessory glands) follows a typical orthopteran organization that has been already stated in numerous studies performed during the past decades (e. g. Spann 1934, Snodgrass 1935, Wigglesworth 1972, Sturm & Pohlhammer 2000). This structural and organizational continuity within the reproductive system of the Orthoptera is invalidated only in one respect: Those species not possessing an ovipositor (e. g. *Gryllotalpa gryllotalpa* Linnaeus 1758) have partly or completely reduced their accessory glands, so that the system has lost one essential component. The existential relationship between ovipositor and accessory glands also confirms the hypothesis outlined in the introduction, according to which the primary function of the accessory gland secretion would consist in the facilitated transport of inseminated eggs through the ovipositor (Sturm & Pohlhammer 2000).

Whilst the receptacular complex with its receptaculum seminis and ductus receptaculi is characterized by a common external morphology among the gryllids (SPANN 1934, DALLAI & MELIS 1966, ESSLER et al. 1992, STURM 2005), a respective interspecific constant concerning shape can not be reported for the accessory glands. As demonstrated by STURM (2002, 2003), the accessory glands are subject to significant shape and size variabilities among the related cricket species Teleogryllus commodus, Gryllus assimilis FABRICIUS 1775, Gryllus bimaculatus DE GEER 1773, and Acheta domesticus LINNAEUS 1758. Those glands with the greatest size (length up to 15 mm) could be found in the mediterranean field cricket G. bimaculatus, whereas the smallest organs (length up to 4 mm) were described for the house cricket A. domesticus. Both the ductus receptaculi and the accessory glands are chiefly marked by the production of secretions having a supporting effect on the reproductive process. Within the ductus the middle region (Dr₂) is responsible for the release of the secretion, whereby single gland cells are arranged in series over a distance of 15 to 20 mm (STURM 2005). Within the accessory glands additionally to the arrangement of single secretory cells in series also a parallel organization of secretion-producing gland sections due to the highly ramified morphology of the organs may be observed. This results not only in an increase of the secretory efficiency, but also in a significant reduction of the glands' lengths (STURM 2002).

As could be successfully demonstrated in the study presented here, the histology and morphology of single components of the female reproductive system in *Teleogryllus* mainly follow a uniform construction scheme including, from outside to inside, a muscle coat, a basal membrane, a central epithelium, and a cuticular intima. As a higly remarkable characteristic of this architecture the epithelium consists of only a single cell layer, where normally all cells are connected to the cuticular intima. Only in the case of the glandular section of the ductus receptaculi, exclusively one cell type, the cuticular-forming cell, within the more differentiated tissue is connected with the cuticular layer. Such a construction plan may be considered as highly characteristic for insects as a whole (Chapman 1998). Hence, the intraspecific uniformity in organ morphology and histology may be extended to an interspecific homogeneity, which could be documented in detail for the accessory glands hitherto (GILLOTT 1998, STURM & POHLHAMMER 2000, STURM 2002).

In future studies morphological and histological investigations of the reproductive sys-

tem and its functionality, which have been carried out comprehensively for the gryllids, will be extended to further families within the Orthoptera to guarantee a stepwise completion of our knowledge concerning the reproductive biology of this fascinating insect order.

Zusammenfassung

Morphologie und Histologie des Reproduktionssystems in Weibchen der australischen Feldgrille *Teleogryllus commodus* WALKER 1869 (Insecta: Orthoptera): Eine zeichnerische Studie – Das Reproduktionssystem der weiblichen australischen Feldgrille *Telegryllus commodus* wurde in morphologischer und histologischer Hinsicht untersucht, wobei verschiedene Zeichnungen auf Basis licht- und elektronenmikros-kopischer Beobachtungen angefertigt wurden. Typisch für orthoptere Insekten setzt sich der Reproduktionstrakt aus paarigen Ovarien, den lateralen Ovidukten, dem medianen Ovidukt, der aus lediglich einem Receptacularkomplex (Receptaculum seminis und Ductus receptaculi) bestehenden Spermatheka, der Genitalkammer und den durch zahlreiche Verästelungen gekennzeichneten akzessorischen Drüsen zusammen. Nach Befruchtung der Oozyten in der Genitalkammer erfolgt deren Abgabe über einen Ovipositor. Einzelne Strukturen des Fortpflanzungssystems sind gemäß einem basalen Bauplan konstruiert, welcher, von außen nach innen betrachtet, eine Muskelschicht, eine Basalmembran, ein einlagiges bzw. einschichtiges Epithel und eine kutikuläre Intima einschließt. Sowohl beim Receptaculum seminis als auch bei den akzessorischen Drüsen bildet die Intima dornen- bis haarförmige Fortsätze aus, die unterstützend auf den Transport der Spermatozoen bzw. des lipophilen Drüsensekrets wirken.

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